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Disruptive selection on male reproductive polymorphism in a jumping spider, Maevia inclemens

Busso, Juan Pablo ; Davis Rabosky, Alison R

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Title :

Disruptive selection on the male reproductive polymorphism in a jumping spider (*Maevia inclemens*)

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Highlights

- Females of *Maevia inclemens* do not show preference for any of the two male morphs.
- Females prefer opposite values of anatomical and behavioral traits for each morph.
- Variation of female preference results in disruptive sexual selection.
- The weak differences between morphs concur with their respective selection pressure.

*Non-highlighted revised manuscript
Click here to view linked References

1 **Title :**

2 **Disruptive selection on the male reproductive polymorphism in a jumping spider (*Maevia inclemens*)**

3

4 **Abbreviated title:**

5 **DISRUPTIVE SEXUAL SELECTION ON PHENOTYPIC POLYMORPHISM**

Abstract

Genetic polymorphism in males has long been considered paradoxical because sexual selection is expected to deplete additive genetic variation. Although studies have shown how divergent selection between populations can make that work, it is very rare to find disruptive selection within one population. Since intersexual selection can have a significant effect on the phenotypic morphospace of the opposite sex, we analyzed the role of female preference as a disruptive selective force. In this study we evaluated how female preference acts on anatomical and sex-related behavioral traits of two male morphs in the jumping spider *Maevia inclemens*. We employed mate-choice trials to analyze the variation of female preference between the two morphs. The tests indicated that females prefer opposite values of two anatomical and two behavioral traits for each male morph. This study is, to our knowledge, the first to show disruptive sexual selection in Arachnidae and significantly expands the realm of disruptive selection, by adding one more case to the very few documented instances. These processes, which act entirely within a species, are of particular interest because they could contribute to the evolution of reproductive isolation and sympatric speciation by sexual selection, a controversial topic in evolutionary biology.

Keywords: Disruptive selection, female preference, sexual selection, male dimorphism, polymorphism, Salticidae

INTRODUCTION

Sexual selection can have a significant influence on the intraspecific phenotypic diversity (Gray & McKinnon, 2007). One of the main components of sexual selection is mate choice, exerted more commonly by females (M. Andersson & Simmons, 2006). Many theoretical models attempt to explain how female preference can drive sexual selection and how it can arise and be maintained (reviewed in M. Andersson & Simmons, 2006; Jones & Ratterman, 2009; Kokko, Jennions, & Brooks, 2006). Generally, these models consider female preference as a fixed trait, and its variability is included as variance around a mean value.

However, female preference is a complex and elaborate component of sexual selection, and it can include substantial variability (Cotton, Small, & Pomiankowski, 2006). This variation in female preference can have a significant effect promoting intraspecific genetic (Birkhead et al., 2006; Neff & Pitcher, 2009; Rowe & Houle, 1996; Tomkins, Radwan, Kotiaho, & Tregenza, 2004) and phenotypic diversity (Cotton et al., 2006; Gray & McKinnon, 2007). Therefore, this variation must be considered as more than just random deviation from a fixed preference in order to understand its influence on the phenotypic evolution of the opposite sex.

In some animals, the morphospace of one sex may exhibit a bimodal or multimodal morphological distribution resulting in alternative phenotypes, which may then adopt alternative reproductive tactics (ARTs; Oliveira, Taborsky, & Brockmann, 2008). These ARTs are more commonly found in males than in females (Michael Taborsky & Brockmann, 2010) and are categorized as bourgeois males, which invest in privileged access to females, and parasitic males that exploit the investment of their bourgeois counterparts (M. Taborsky, 1997; Michael Taborsky & Brockmann, 2010). While females prefer bourgeois males, thereby exerting intersexual selection on them, the parasitic males circumvent such preference (Gross, 1991; Shuster & Sassaman, 1997; Watson & Simmons, 2010).

These alternative phenotypes can result from two or more genotypes reacting differently to a particular environmental threshold value (Michael Taborsky & Brockmann, 2010). These genetic polymorphisms in males has long been considered paradoxical because sexual selection is expected to deplete additive genetic variation (Kirkpatrick & Ryan, 1991; P. D. Taylor & Williams, 1982). Gray and McKinnon (2007) highlighted that the maintenance of polymorphism in most cases is due to divergent selection between populations, and there is very little evidence of disruptive selection within populations. However, disruptive selection has exciting ecological significance in this context because it could drive sympatric speciation, a mode of speciation under controversy (Sergey Gavrilets & Hayashi, 2005; Gray & McKinnon, 2007; van Doorn, Dieckmann, & Weissing, 2004). Normally studies focusing on polymorphic species address the mechanisms that stably maintain the morphs in nature, such as negative frequency dependent selection (Kokko, Jennions, & Houde, 2007; Maynard Smith, 1982; Zajitschek & Brooks, 2008); however, we are testing something different here. We address the role of selection (through female preference) as a disruptive force widening the phenotypic differences between morphs, not the stable maintenance of these strategies. To analyze the role of female preference as a disruptive selective force on polymorphic males, it is important to target a system where intersexual selection can have a significant effect on the mating success of the different morphs.

Taxa with a large diversity of sexual signals are especially affected by sexual selection on the reproductive success and phenotypic traits of the opposite sex (Arnqvist, Edvardsson, Friberg, & Nilsson, 2000; Barraclough, Harvey, & Nee, 1995; O. Seehausen, 2000). In jumping spiders (Araneae: Salticidae), males display a wide variety of vibrant colors (L. A. Taylor & McGraw, 2007) and extremely elaborate vision-mediated courtship displays (Clark, 1994; D. O. Elias, Maddison, Peckmezian, Girard, & Mason, 2012). This large diversity of signals is possible because salticids have the highest resolution single-chambered corneal eyes in Araneae (Blest, Ocarroll, & Carter, 1990; M. F. Land, 1969a, 1969b; Michael F Land & Nilsson, 2012) with a spatial acuity surpassing that of many birds and approaching that of

primates (Harland & Jackson, 2000; M. F. Land, 1972, 1974; Williams & McIntyre, 1980). The elaborate courtships together with the acute vision would allow female preference to act as a selective force on male traits in this taxon. Furthermore, Masta and Maddison (2002) reported that spatial variation in female preference in *Habronattus pugillis* (Araneae: Salticidae) resulted in diversifying selection on male sexual traits, causing a divergence in males' coloration and behavior between different populations. Therefore, salticid spiders are an excellent study system for addressing questions related to sexual selection and female preference in particular.

We focused on one salticid species from the Eastern and Midwestern United States, *Maevia inclemens* (Araneae: Salticidae), in which female choice plays an important role in the males' mating success (Clark & Uetz, 1992; Peckham & Peckham, 1889). Although there is one female morph, this species presents two male ARTs between two discrete, genetically determined male morphs: the Grey (G) morph and the Tufted (T) morph (Clark, 1992). These morphs are found in nature in a 1:1 ratio, and present a discrete bivariate morphospace, since there are no mosaic or intermediate phenotypes in the species (Peckham and Peckham, 1889; Painter, 1913; Clark, 1992) . The phenotypes have very similar anatomical characteristics during early development, but when reaching sexual maturity, they differ considerably in their coloration pattern and initial courtship phase (Fig. 1 and video link in the legend; Clark, 1994). The courtship patterns and proximity to the female are optimal for each morph to attract female attention (Clark & Morjan, 2001; Clark & Uetz, 1993). The G morph has striped legs, yellow pedipalps and orange spots on the abdomen (Fig. 1a). Its courtship initiates at 3 cm from the female and consists of crouching down and pointing its first and second pairs of legs forward (adopting the shape of an arrow) while gliding sideways in receding semi-circles in front of the female (Fig. 1c). On the other hand, the T morph has a completely black body, with white legs and three tufts above the anterior median eyes (Fig. 1b). During the initial courtship phase, 9 cm away from the female, the male stands up by stretching the last three pairs of legs and points the forelegs upwards while waving them vigorously

by rapid flexion and extension (Fig. 1d). Meanwhile, it also waves its pedipalps up and down and swings the abdomen, which points downwards, in a semi-circular pattern. Hence, in contrast to many other species with ARTs where sneak copulation undermines female mate choice as a factor determining population differentiation (Magurran, 1998), in *M. inclemens* there is no parasitic tactic because both morphs invest in courtship, although employing different dances (Hoefler, 2008). Consequently, this salticid provides an excellent opportunity to analyze the disruptive role of female preference on male traits. Since in *M. inclemens* both discrete bourgeois tactics present clear differences in traits related to sexual communication (coloration and courtship) and female choice plays an important role in male mating success (Clark & Uetz, 1992; Peckham & Peckham, 1889), we hypothesized that in this species disruptive female preference could be influencing the intraspecific male phenotypic diversity. Based on this, we predicted that the females would prefer for each morph opposing values of the same trait, widening the phenotypic differences between them. In this study we employed mate-choice trials to analyze the variation of female preference between the two morphs and used standardized regressions to generate univariate linear selection differentials to assess the intensity and variation of sexual selection by female preference on the anatomical and behavioral traits of the morphs.

METHODS

Collection of Specimens and Surveying Morph Frequencies

We collected specimens (114 males and 100 females) in natural areas in Ann Arbor, Michigan, United States from May to June in 2012 (corresponding to the reproductive season). We collected them at the ecotone between forest and grassland, because that's where they commonly occur (Clark, 1992). Both males and females were collected using sweep netting (Clark & Biesiadecki, 2002).

Maintenance of Specimens

All specimens collected during field surveys were housed individually in acrylic boxes (10 cm x 10 cm x 20 cm) within a climate chamber on a 14:10 h light:dark cycle at 25 ºC. We provided each individual with water in cotton-stoppered vials and fed them twice a week with a mix of *Drosophila* species (*D. melanogaster, D. virilis, D. americana* and *D. novamexicana*). The individuals were visually isolated from each other to avoid the influence of neighboring males on the females. The spiders were housed individually to avoid cannibalism, and we enriched the environment of the spiders by adding twigs and leaves to the cages, which is important to avoid alteration of the spiders' behavior (Carducci & Jakob, 2000). Individuals were checked daily to monitor molting. Once the spiders had successfully accomplished their last molting, indicating that they've reached sexual maturity, they were employed in our experiments. Maturity is recognizable in the males due to their marked dimorphic phenotypic traits as adults and in females due to their hardened sclerotized epigynum.

Female Preference and Courtship Characteristics

To assess how the intersexual encounters take place in nature, we created female dummies, by killing 4 females and placing them in natural pose, resembling the live females. The dummies were sprayed with a clear acrylic coating to fix the females in that pose. We then placed the dummies in those field locations, where females were previously captured. We situated a video camera 1.5 m above the dummy and recorded 8 hours per day for three days. In all instances, we observed males approach the dummies, but only one at a time and two males never approached simultaneously. Courting was sometimes observed but not always, presumably due to the lack of reaction of the female dummy, and in some instances the approaching males even attempted to copulate with the female dummy. Additionally, previous studies also report encounters in the field between only one male and one female (Clark, 1992). Hence, to simulate the natural conditions, we decided to analyze female preference using

mate-choice tests with only one male (Hebets, 2003). The female had the choice to mate or not, and by placing only one male per trial, female choice is based only on the traits of that one male she encounters, as it seems to be the natural scenario for the species. A two-choice test would have been suitable to determine which individual has a mating advantage when confronted to another male; however, this has been tested in the past and found no difference in mating success between the morphs (Clark & Biesiadecki, 2002; Clark & Morjan, 2001). In this study we wanted to address which male traits where being preferred by the females and if this preference was different for the different morphs. Furthermore, we decided against a two-choice test, because in this scenario the preference would actually depend on the traits of both contestants, impeding to disentangle which trait of which male influenced the choice, or if the interaction between males influenced the choice.

The tests were carried out during the reproductive season, from May to June. We used only mature virgin females that had not oviposited eggs before the trial (N = 44). Females with these characteristics were the limiting factor in our sample size. Virginity of the individuals was easy to determine, since they matured in isolation in the lab, and they are unable to mate before reaching maturity. Prior to each trial, we weighed individuals of both sexes on an electronic scale (SI-124, Denver Instruments) with a precision of 0.1 mg. We also photographed the individuals from above with a DSC-HX1 (Sony) camera. They were photographed on top of a millimeter paper sheet, which worked as the scale for the morphological measurements. We measured the width of the prosoma from dorsal photographs employing Photoshop CS6 (Adobe).

The mate-choice tests were carried out in circular arenas, built with two stacked cardboard hollow cylinders of 203.2mm diameter and 150 mm in height. We placed a sheet of millimeter paper between the cylinders to provide a suspended substrate for the transmission of the vibrations, which are an important component of the salticids male courtship (Damian O. Elias, Sivalinghem, Mason, Andrade, & Kasumovic, 2010). The inner wall of the cylinder was covered with petroleum jelly to

prevent the individuals from escaping from the arena. Additionally, we placed a foam ring between each cylinder and the millimeter paper sheet to avoid the transmission of external vibrations that could be picked up by the cylinders. The arena was placed over a foam sheet to isolate from possible vibrations of the bench on which we worked. Since *M. inclemens* detects light in the UV range (Peaslee & Wilson, 1989), we illuminated the arena with a bulb emitting light in the visual and UV spectrum (26 W ReptiGlo 5.0).

For each trial, we placed a new millimeter paper sheet as the substrate of the arena and we also wiped the walls of the arena with ethanol to remove any residues, and avoid the influence of silk and pheromones from previous encounters. We placed a female in the arena and allowed 20 minutes of acclimation. Afterwards, we placed a randomly selected male into the arena. Because preliminary work on this species showed that 20 minutes were sufficient time for matings to start (data not shown), the encounters lasted until mating occurred or else 20 minutes had elapsed. We defined successful mating as the insemination of both of the female's spermathecae and insemination as the insertion of the embolus into one of the spermathecae.

The encounters were recorded with two video cameras (Sony HDR-CX160). One was fixed above the arena and the other one was held by hand. The latter allowed us to zoom in and focus on the male behaviors from the most suitable angle, providing a larger and clearer image of the behaviors. Out of the 44 trials, 26 were done with G males and 18 with T males. The discrepancy between the number of males captured in the field and the ones employed in the experiment are due to survival and to the fact that not all of them were captured as juveniles; hence, these adult males were counted for the morph ratio but not employed in further experiments.

To evaluate female preference, we scored the male mating success [presence/absence of mating] (Clark & Biesiadecki, 2002). We also analyzed the differences in female preference for anatomical traits (weight, prosoma width and body condition) and behavioral traits of each morph:

detection latency (time elapsed until the male detected the female), detection distance, courtship latency (time elapsed since the male detected the female until it began courting) and number of courtship events (until mating started). Detection of the female was defined as the male turning its prosoma to point the anterior median eyes towards the female. Since the males detected the female shortly after the trial was started (Table 1), and started courting on average within the first two minutes, signaling his willingness to copulate, a lack of copulation after 20 minutes reflects the female reluctance to mate with that male.

Statistical Analyses

We evaluated if the morph ratio in the field differed from 1:1, employing a X^2 Goodness-of-fit test. We further analyzed the differences in the anatomical and behavioral traits between the morphs in an ANOVA for each trait, to determine if they differ in traits other than the courtship traits described by Clark (1994). In these models the trait was always the response variable and the predictor was the factor morph. However, body weight is a proxy for both body size and body condition; hence, to disentangle these two effects, we looked at weight alone, and also combined with prosoma width (another proxy for body size). The combined model was to evaluate the body condition differences between morphs, and we employed an ANCOVA with weight as the response variable, morph as a predictor and included prosoma width as covariate to control for body size (Freckleton, 2002; García-Berthou, 2001). The width of the prosoma was elevated to the third power, to be able to link a volumetric measurement (weight) with a linear measurement of body size: prosoma width (Jakob, Marshall, & Uetz, 1996). This ANCOVA accounts for the weighted average of the regression coefficients within groups and properly estimates the error degrees of freedom, reducing the Type I error rate. The *F* and *P*-value for body condition in Table 1 were extracted from the ANCOVA. However, this ANCOVA does not allow an easy numerical or graphical representation of the body condition. Consequently, due to the similarity between the

ANCOVA and ANOVA of the residuals (Winer, Brown, & Michels, 1971), and to simplify the numerical and graphical representation of the body condition, the morph estimates in Table 1, and Fig. 2 were elaborated from the residuals of the regression between body mass and the width of the prosoma to the third power. The ANCOVA is the proper statistical analyses for the condition differences, but the ANOVA of the residuals illustrates these condition differences in a comprehensible manner. While the morph ratio test included the 114 individuals collected in the field, the ANOVA tests and ANCOVA test for morph differences included only the 44 individuals employed in the choice tests.

We evaluated the mating success difference between the morphs employing a X^2 Goodness-of-fit test. Additionally, to analyze if female body size influences their mating preference, we tested for size-assortative mating between males and females in an ANCOVA with male weight as the response variable, and the predictive variables were female weight, mating success as a factor [1 or 0], and the interaction between them. In this analysis, the insignificance of the female weight covariate would show that the females were paired randomly with males of any size in the experiment, and not based on their size. On the other hand, a significant interaction between female weight and the mating success factor would show that the male weight:female weight slope differs between paired and unpaired females and therefore evincing an influence of female size on their mating preference :size-assortative mating.

To ensure that the male traits measured in the mate-choice experiment were independent from each other, we elaborated a correlation matrix between all traits measured and calculated their significance. A lack of significant correlation suggests that the traits are independent, and that we are not measuring the same trait with different variables.

We assessed the intensity and variation of female preference for the anatomical and behavioral traits of the morphs by employing standardized regressions to generate univariate linear selection differentials (Arnold & Wade, 1984; Lande & Arnold, 1983). This method provides standard selection coefficients, which allow the comparison of selection strength between different traits and between

different species, even if they have employed other proxies for fitness. The standardized values for the response variable (mating success) are obtained by transforming it to a relative fitness, and for the predictive variables (anatomical and behavioral male traits) by transforming them to standardized Z-scores. Relative fitness expresses the fitness of each individual relative to the fitness of the other individuals in the sample. Hence, the rarer the mating events are in the sample, the larger the fitness of a mating individual is relative to its peers. Relative fitness was calculated as the absolute fitness component (i.e., mating success [1 or 0]) over the sample mean fitness (number of successful matings divided by the total number of trials) (Arnold & Wade, 1984). We then calculated standardized Z-scores for each of the predictive anatomical and behavioral variables by subtracting the sample mean from each value and dividing the difference by the standard deviation: $z_i = (x_i - \bar{x})/SD_x$. Significance testing of the variation of female preference for the different traits was performed using a GLM including the relative fitness as a response variable, and as predictors: the standardized trait being analyzed, the factor morph, and the interaction term. The only exemption to this model was the analysis of the variation of female preference for male body condition, where we employed a GLM with relative fitness as the response variable, and the predictors were the weight of the males, the factor morph, the interaction term, and prosoma width as covariate to control for body size, since it is the proper statistical model for calculating body condition (Freckleton, 2002; García-Berthou, 2001), as noted for the ANCOVA for body condition explained above. The reference level for all GLM analyses was the G morph. Between-morph variation in selection through female preference in all cases is established by significant variable-by-morph interactions, i.e. a significant interaction indicates that the direction of selection is significantly different between the morphs for that particular trait. To control for the rate of false positives in multiple hypothesis testing, we pooled all *P*-values and calculated *Q*-values for combined false discovery rate (John D Storey, 2002; John D. Storey, 2003). Hence, here we report both the *P*-values and the *Q*-values, which are the adjusted *P*-values found using an optimized false discovery

rate approach (John D Storey, 2002; John D. Storey, 2003). Significance was considered as a *Q*-value lower than 0.05. All analyses were done using the software R Version 3.2.2 (R Core R Development Core Team, 2015).

RESULTS

The morph ratio in nature was not significantly different from the unity (G males = 60, T males = 54, X^2= 0.316, *P* = 0.575). In our experiments, the male morphs did not differ significantly in their mating success (X^2= 0.876, $N_{G\ males}$ = 26, $N_{T\ males}$ = 18, *P* =0.349), nor in any of the anatomical and behavioral variables recorded in this study, except for the expected difference in the courtship distances (Table 1). We did not find a correlation between male and female weights in our experiment ($Weight_{Fem}$: $F_{1,39}$ = 1.317, *P* = 0.258) indicating that males and females were paired with each other randomly, and not based on size. We also did not find assortative mating in *M. inclemens*, since the regression between male and female weight did not vary significantly between paired and unpaired females ($Weight_{Fem}$*Mating success: $F_{1,39}$ = 1.200, *P* = 0.280), meaning that female weight did not influence female preference, i.e.: females of all sizes paired with males of all sizes.

Among the male traits we measured, we found only two significant correlations: weight with prosoma width and with body condition, while the rest showed insignificant correlations (Table 2). These correlations are addressed in the discussion, while the rest of the uncorrelated male traits were treated as independent.

Regarding the linear selection differentials, the morph factor was significant in only two anatomical variables: weight and body condition. These variables also showed a significant interaction with the morph factor (weight by morph, Likelihood Ratio X^2= 5.056, *Q* = 0.043, Fig. 2a; and body condition by morph, Likelihood Ratio X^2= 9.942, *Q* = 0.022; Fig. 2b).

Among the behavioral variables, males that detected the females earlier had greater mating success (Likelihood Ratio X^2= 7.940, Q = 0.022; Table 3). Courtship latency also influenced mating success significantly (Likelihood Ratio X^2= 7.579, Q = 0.022; Table 3), but it also interacted significantly with the factor morph (Likelihood Ratio X^2= 5.115, Q = 0.041; Fig. 2c). The number of courtship events each male performed also interacted significantly with the factor morph (Likelihood Ratio X^2= 5.204, Q = 0.041; Fig. 2d). The significant interactions between the male traits and morph are indicative of different selection forces acting on the two morphs (Fig. 2).

DISCUSSION

Here we provide the first evidence of disruptive intersexual selection acting in spiders, since in *M. inclemens* female preference for male traits varied significantly between morphs. Females preferred opposite values of two anatomical (weight and body condition) and two behavioral traits (courtship latency and number of courtship events) for each male morph. The opposing direction of these selection forces acting on the male morphs are indicative of intraspecific disruptive sexual selection.

Females preferred lighter G males and heavier T morph males. However, weight is a proxy for both body size and condition. By including weight and prosoma width together in the model for body condition, we could disentangle both effects on the mating success. Keeping in mind that the G morph is always the reference level in our GLM analyses, the significant negative interaction between prosoma width and morph together with the significant positive interaction between weight and morph, indicate that the females prefer T males with higher weights relative to their body size, i.e. T males of higher condition. In contrast, they prefer G males of lower condition. Hence, in *M. inclemens* there is disruptive female preference for body condition of the males, which is also reflected in the disruptive female preference for male weight.

Regarding the courtship-related traits, females were most likely to mate with G males with shorter courtship latencies and more courtship bouts, or with T males that waited longer to start courting and courted less times. In our study all individuals were exposed to the same conditions in the reproductive arena, making it unlikely that the disruptive selection is due to environmental variation. Furthermore, Clark (1992) observed no differences between the morphs in habitat selection or activity level in their natural environment, suggesting shared signaling environments and costs of choice between the morphs within a population, which makes it improbable that these factors could have affected the within population variation in mate preference we observed (Arnegard & Kondrashov, 2004). Consequently, the opposing female preference for courtship traits of each morph also suggests intraspecific disruptive selection by female preference.

This disruptive female preference acting concurrently on several independent anatomical and behavioral traits of the male morphs is accordant with the discrete phenotypic division of the morphospace in *M. inclemens*. It is interesting to note that out of the 114 males collected in our study, none belonged to an intermediate or mosaic phenotype. Furthermore, there are also no reports of intermediate phenotypes from previous work on this species (Peckham and Peckham, 1889; Painter, 1913; Clark, 1992) . These discrete morphs differing mainly in coloration pattern and courtship displays suggest the existence of a force maintaining the distinct differences between the morphs. It has been shown that variation in female preference can influence the diversification of male courtship signals and promote speciation (Guerra & Ron, 2008). Furthermore, variation in female preference in *H. pugillis*, a jumping spider, resulted in diversifying selection on male sexual traits, causing a divergence in males' coloration and behavior between different populations (Masta & Maddison, 2002). It is possible that the disruptive selection by female preference in *M. inclemens* is involved in the intraspecific phenotypic divergence between the morphs.

There may be advantages related to the intraspecific diversification of male traits by female preference. Since in *M. inclemens* male morphs are determined genetically (Clark, 1992), a disruptive female preference would help widen the differences between the morphs, facilitating the recognition by females of the different male genotypes, allowing females, through alternating matings between morphs, to easily increase the genetic diversity of their offspring. An increase in offspring diversity increases also the fitness of the female (Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003; Forsman, Ahnesjö, & Caesar, 2007). Furthermore, this increase in genetic diversity decreases inbreeding (Johnson et al., 2010), thus preventing severe fitness depression (Bilde, Maklakov, & Schilling, 2007; Saccheri, Brakefield, & Nichols, 1996). Our data does not allow us to analyze this hypothesis, since we only looked at one mating; however, future studies with *M. inclemens* addressing multiple matings and offspring survival could address the fitness benefits for the females of an increase in offspring genetic diversity, resulting from mating with both male morphs. Another advantage for the disruptive female preference on male traits would be a reduced predation risk. Predators often focus their attention selectively on recently and commonly encountered prey items while ignoring the alternatives (A. B. Bond & Kamil, 1999, 2002; Jackson & Li, 2004). Hence, dividing the male population into two morphs would decrease the probability of predators forming search-images for them, as observed for visual predators (Alan B. Bond, 2007; Karpestam, Merilaita, & Forsman, 2014, 2016). In *M. inclemens*, it is more advantageous to present dimorphism in males rather than in females, since males are the most active sex (Clark, 1992), which increases the chances of encountering a predator. Our study does not permit the evaluation of these possible advantages, and ecological studies addressing predation risk of the morphs in *M. inclemens* are required to directly examine this issue. Nevertheless, all these benefits are not mutually exclusive and they would all favor disruptive selection of male traits by female preference.

Although in our study the two male morphs did not differ significantly in the four traits under disruptive selection, they showed some weak differences concordant to the selection pressure for each morph in those four traits. The lack of differences was due to considerable variation within morphs, in spite of all individuals being of similar age. This lack of divergence was also witnessed in other taxa, in which disruptive selection due to mate choice was reported (Greene et al., 2000; Sappington & Taylor, 1990; Stelkens et al., 2008). There are however different possibilities explaining why we did not pick up a significant difference between the morphs for the traits under disruptive selection. That preferences for condition-dependent traits are less directly responsive to sexual selection (Arnegard & Kondrashov, 2004) may explain why we did not observe differences for weight and body condition between morphs. Another explanation could be low heritability in these traits (Emlen, 1994), which in itself does not reject the possibility of an underlying genetic basis. Furthermore, previous evolutionary responses could weaken selection (Rueffler, Van Dooren, Leimar, & Abrams, 2006). Alternatively, traits under disruptive selection might be correlated with other traits that are under different forms of selection, thereby counteracting disruptive selection (Gray & McKinnon, 2007). One or more of these processes could be occurring simultaneously on this species, affecting selection on the morphospace of the males.

In our study we measured the mating success of the individuals as proxy for reproductive success, one of the main components of fitness. Neither morph showed a mating advantage in our study nor in previous studies (Clark, 1994; Clark & Biesiadecki, 2002), which suggests that sexual selection may not favor the existence of either one over the other. These results evince consistency of the female preference across different populations and time, and also confirms that our experimental setting, although different from the one employed by Clark (1994), shows the same female sexual preference. Unfortunately, there are no records of these mating interactions in nature to compare these results to a natural setting. However, since the morphs are genetically determined (Clark, 1992) and produce equal number of offspring (Clark & Biesiadecki, 2002), their equivalent mating success in the experiments

would hint a 1:1 morph ratio, which is in agreement with the 1:1 ratio found in nature in this and in previous studies (Painter, 1913; Clark, 1992) . Nevertheless, in our weight and body condition models, we observed that when controlling for weight, the mating success of the morphs differed significantly, and the T males had a higher mating success. In this case, we would not expect a 1:1 morph ratio in nature, unless other selection forces would affect differently the survival of each morph compensating their uneven mating success. Survival, the second component of fitness, can also affect the morphospace of polymorphic species (A. B. Bond & Kamil, 2002; Gray & McKinnon, 2007), but until now there is no evidence of how selection forces affect the survival of the morphs in *M. inclemens*. Further studies addressing the influence of selection on the survival of the morphs would complement our intersexual selection results, providing a holistic picture of the forces shaping the morphospace of this jumping spider.

To our knowledge, this study is the first to show intraspecific disruptive sexual selection in Arachnidae, providing an important contribution to an otherwise short list of examples of this process overall (Greene et al., 2000; Sappington & Taylor, 1990; Stelkens et al., 2008). It has been suggested that polymorphism and phenotypic divergence in species with ARTs could be the starting point of speciation (Corl, Davis, Kuchta, & Sinervo, 2010; Wittkopp et al., 2009). By acting entirely within a species, disruptive selection is of particular interest because it could contribute to the evolution of reproductive isolation and sympatric speciation by sexual selection, a phenomenon that currently remains controversial in evolutionary biology (Sergey Gavrilets & Hayashi, 2005; van Doorn et al., 2004). Sexual selection is generally assumed to play a direct role in the diversification of sexual traits (B. Andersson, 1994; Eberhard, 2010) and is considered an important diversifying process (S. Gavrilets, 2000; Panhuis, Butlin, Zuk, & Tregenza, 2001). Furthermore, variation in female preference can also act as a diversifying selective force (Janette Wenrick Boughman, 2001; J. W. Boughman, 2002; Ole Seehausen et al., 2008). In many studies, it has been observed that there is a correlation between species richness and traits

404 involved in sexual communication or sexual selection, suggesting the role of sexual selection in
405 speciation (Arnqvist et al., 2000; Barraclough et al., 1995; Mank, 2007; Owens, Bennett, & Harvey, 1999;
406 O. Seehausen, 2000). With over 5000 species, Salticidae is the most speciose family of the 114
407 recognized families in Araneae (Platnick, 2016). Additionally, jumping spiders have acute eyesight
408 (Harland & Jackson, 2000; M. F. Land, 1972, 1974; Williams & McIntyre, 1980), and males present
409 vibrant coloration (L. A. Taylor & McGraw, 2007) and elaborate courtship displays (Clark, 1994; D. O.
410 Elias et al., 2012). Because of these characteristics, female preference could play a pivotal role in the
411 diversification of this taxon and contribute to its dramatic radiation. It would now be interesting to
412 examine the specific role of variation in female preferences in the speciation processes of the Salticidae.

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FIGURE LEGENDS:

Figure 1. Male morphs and phase I of the courtship displays. a) Grey (G) morph (Courtesy of Thomas Shahan). b) Tufted (T) morph (Courtesy of Matt Versweyveld). c) Phase I of courtship of the G morph and d) Phase I of the T morph courtship. Courtship video: https://www.youtube.com/watch?v=C5YidaWxt8Q&feature=youtu.be .

Figure 2. Female Preference. Variation in female preference between the male morphs (*N* = 44 females). All panels show a significant interaction between the morph and the trait under selection, which is indicative of disruptive selection between the morphs. a) Male weight (mg). b) Body condition index. c) Courtship latency (in seconds). d) Number of courtship events.

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Figure

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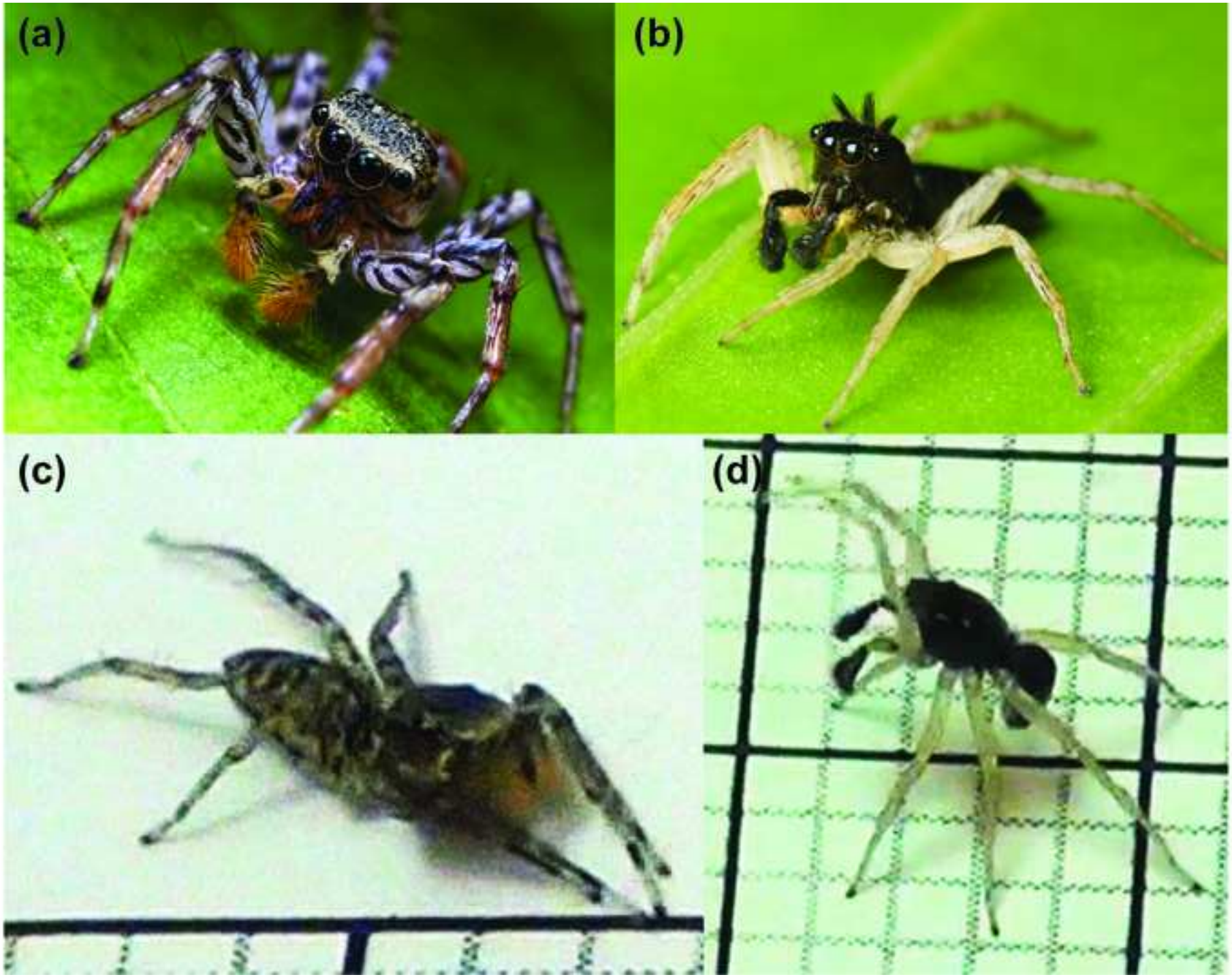

Figure
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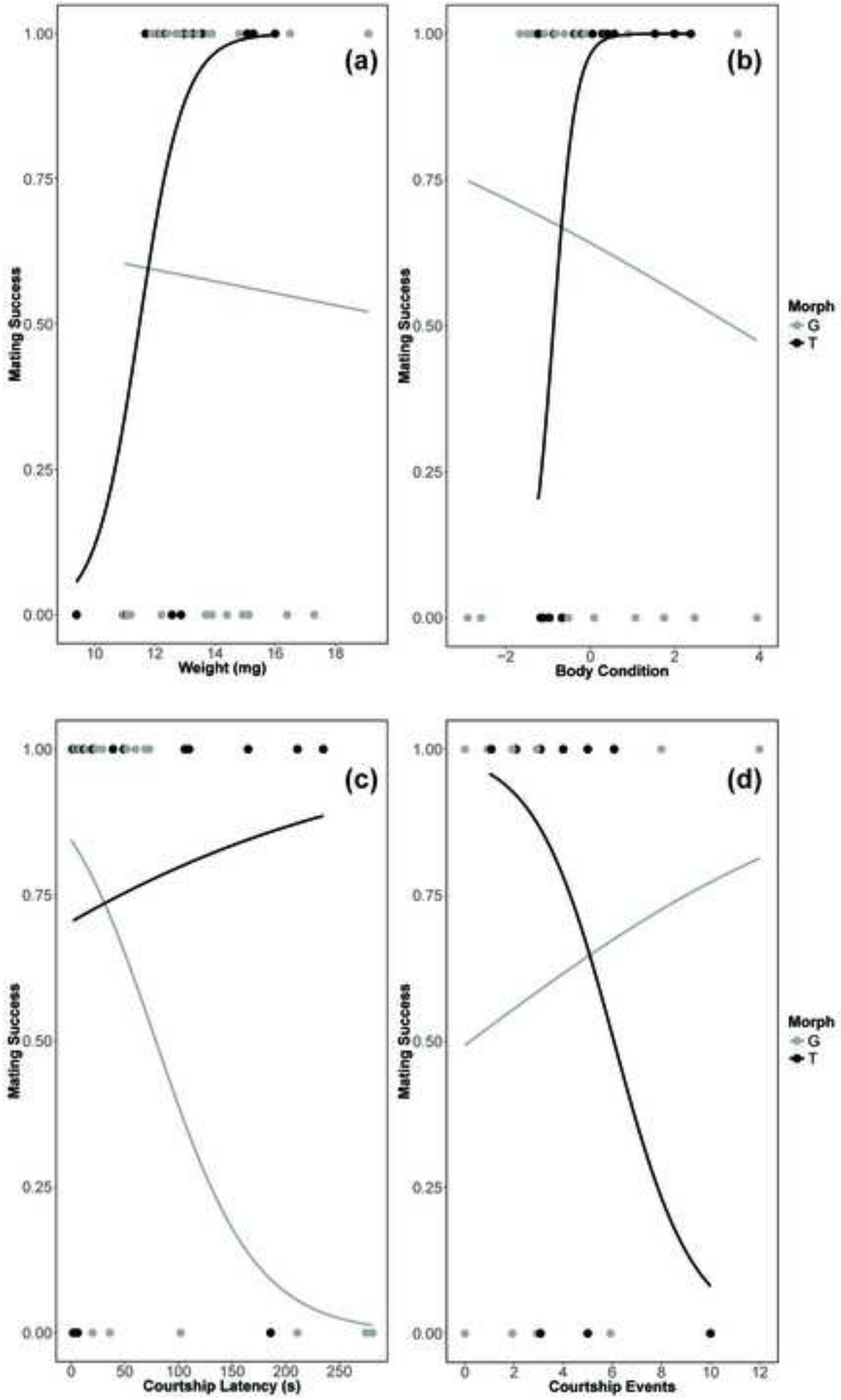

Table 1. Morph differences in anatomical and behavioral traits.

Trait	G Morph	T Morph	*F* -value	*P* -value
Weight (mg)	12.791 ± 0.383	13.192 ± 0.344	0.562	0.456
Prosoma width (mm)	1.91 ± 0.021	1.943 ± 0.019	1.261	0.266
Body Condition	-0.036 ± 0.251	0.021 ± 0.303	0.008	0.999
Detection latency (s)	27.784 ± 7.681	29.182 ± 6.196	0.016	0.900
Detection distance (mm)	123.726 ± 9.064	136.333 ± 11.823	0.698	0.407
Courtship latency (s)	55.286 ± 12.599	105.191 ± 30.173	3.090	0.084
Courtship events (s)	3.406 ± 0.426	3.228 ± 0.47	0.073	0.788
Courtship distance (mm)	74.085 ± 3.939	87.837 ± 5.573	4.163	0.046*

The mean and SE for each morph are presented with their corresponding significances (G males, N = 26; T males, N = 18). Statistically significant results are indicated with an asterisk.

Table

Table 2. Correlation matrix between male traits.

	Weight (mg)	Prosoma width (mm)	Body Condition	Detection latency (s)	Detection distance (mm)	Courtship latency (s)	Courtship events
Prosoma width (mm)	0.58 (<0.001)						
Body Condition	0.82 (<0.001)	0.02 (0.861)					
Detection latency (s)	0.14 (0.326)	0.03 (0.842)	0.16 (0.261)				
Detection distance (mm)	-0.03 (0.811)	0.11 (0.453)	-0.12 (0.397)	-0.02 (0.889)			
Courtship latency (s)	0.1 (0.501)	0.15 (0.304)	0.01 (0.951)	0.15 (0.282)	0.15 (0.314)		
Courtship events	-0.13 (0.354)	-0.12 (0.409)	-0.08 (0.547)	-0.1 (0.471)	0.08 (0.578)	-0.28 (0.063)	
Courtship distance (mm)	0.05 (0.756)	-0.11 (0.440)	0.15 (0.317)	0.06 (0.662)	0.03 (0.842)	-0.16 (0.268)	0.14 (0.348)

The correlation between the two variables is presented with their corresponding significance in parenthesis. (G males, N = 26; T males, N = 18).

Table

Table 3. Estimates of the standardized regression models.

Selected Trait	Variable from Selection Model	Estimate ± SE	LR Chi-Square	*P* -value	*Q* -value
Weight (mg)	Weight (mg)	-0.030 ± 0.135	0.042	0.838	0.433
	Morph	0.393 ± 0.233	4.812	0.028*	0.043*
	Weight (mg) * Morph	0.443 ± 0.252	5.056	0.025*	0.041*
Prosoma width (mm)	Prosoma width (mm)	0.235 ± 0.142	2.565	0.109	0.112
	Morph	0.416 ± 0.241	2.977	0.084	0.098
	Prosoma width (mm) * Morph	-0.046 ± 0.251	0.001	0.974	0.472
Body Condition	Prosoma width (mm)	0.323 ± 0.156	0.801	0.371	0.074
	Morph	0.410 ± 0.231	6.782	0.005**	0.022*
	Weight (mg)	-0.176 ± 0.148	9.942	0.264	0.221
	Prosoma width (mm) * Morph	-0.537 ± 0.330	6.510	0.011*	0.028*
	Weight (mg) * Morph	0.750 ± 0.334	10.186	0.001**	0.015*
Detection latency (s)	Detection latency (s)	-0.340 ± 0.122	7.940	0.005**	0.022*
	Morph	0.275 ± 0.216	1.923	0.165	0.160
	Detection latency (s) * Morph	0.367 ± 0.251	2.832	0.092	0.100
Detection distance (mm)	Detection distance (mm)	-0.133 ± 0.143	0.863	0.353	0.262
	Morph	0.268 ± 0.245	1.399	0.237	0.207
	Detection distance (mm) * Morph	-0.080 ± 0.260	0.206	0.65	0.374
Courtship latency (s)	Courtship latency (s)	-0.406 ± 0.141	7.579	0.006**	0.022*
	Morph	0.340 ± 0.226	1.118	0.29	0.232
	Courtship latency (s) * Morph	0.508 ± 0.22	5.115	0.024*	0.041*
Courtship events	Courtship events	0.117 ± 0.134	0.706	0.401	0.267
	Morph	0.339 ± 0.225	2.962	0.085	0.098
	Courtship events * Morph	-0.511 ± 0.241	5.204	0.023*	0.041*
Courtship distance (mm)	Courtship distance (mm)	0.010 ± 0.161	0.004	0.947	0.471
	Morph	0.190 ± 0.260	0.688	0.407	0.267
	Courtship distance (mm) * Morph	-0.168 ± 0268	0.531	0.466	0.293

The estimate of each variable in each model and the interaction with their respective Likelihood Ratio X^2 value significance. The significant interactions between the factor morph and the variable of the model indicate differential selection for that trait. Statistically significant results are indicated with asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The same applies for the Q -values.